Environmental change influences the life history of salmon *Salmo salar* in the North Atlantic

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Running head: Atlantic salmon at sea

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Together, climate and food availability are main drivers of change in the ecology of species. The recent changes in size and age at maturity of Atlantic salmon *Salmo salar* of the River Imsa appear to be an example of that. Annual mean total length (L_T) of wild one-sea-winter (1SW) *S. salar* decreased from 63 cm to 54 cm, and there was a corresponding decrease in condition factor (*CF*) for cohorts migrating to sea from 1976 to 2010. The reduction in L_T is associated with a 40 % decline in mean individual mass, from 2 kg to 1.2 kg. Released hatchery fish reared from parental fish of the same population, exhibited similar changes from 1981 onwards. The decrease in L_T correlated negatively with near-surface temperatures in the Eastern Norwegian Sea, the main feeding area of the present stock. Furthermore, *S. salar* exhibited significant variations in the proportion of cohorts attaining maturity after only one winter in the ocean. The proportion of *S. salar* spawning as 1SW fish was lower both in the 1970s and after 2000 than in the 1980s and 1990s associated with a gradual decline in post-smolt growth and smaller amounts of reserve energy in the fish. In wild *S. salar*, there was a positive association between post-smolt growth and the sea survival back to the River Imsa for spawning. In addition, among smolt year-classes there were significant positive correlations between wild and released hatchery *S. salar* in L_T, *CF* and age at maturity. The present changes may be caused by ecosystem changes following the collapse and rebuilding of the Norwegian spring spawning herring *Clupea harengus* population, a gradually decrease in zooplankton abundance and climate change with increasing surface temperature in the Norwegian Sea. Thus, the observed variation in life history traits of *S. salar* appears primarily associated with major changes in the pelagic foodweb in the ocean.

Keywords: climate, condition factor, environmental change, growth, sea survival, temperature.

INTRODUCTION

Climate is a governing variable of the biosphere, and the ongoing climate change has serious effects on Earth's ecosystems. With a nearly 1°C rise in global warming experienced during the past century, significant shifts in distribution, phenology, behaviour and life history of organisms are already evident (Parmesan & Yohe, 2003). With an expected increase up to 7°C by 2100, the earth's biota will be even more seriously affected (Sheridan & Bickford, 2011).

Increasing temperature accelerates biochemical and physiological processes of poikilothermic organisms and affects their body size (Clarke, 2003; Pörtner & Farrell, 2008). The 'temperature – size rule' states that there is tendency for poikilotherms to grow faster, but reach adulthood earlier, at a smaller body size in a warmer climate (Atkinson, 1994; Zou *et al.,* 2012). Consistent with this rule, several recent studies have demonstrated smaller sizes of poikilotherms associated with climate warming (*e.g.* Daufresne *et al.,* 2009; Ohlberger *et al.,* 2011; Sheridan & Bickford, 2011). This contrasts the effect when developmental rate is stimulated by increased food quality, where organisms will mature larger, not smaller, for their age (Berrigan & Charnov, 1994). This differing effect between higher temperature and better food quality on body size, called 'the Berrigan & Charnov's life-history puzzle', has received much attention in ecological literature (*e.g.* Perrin, 1995; Jonsson et al., 2013, Trip *et al.,* 2014).

Growth rates of fishes fed to satiation increase with temperature up to a maximum point denoted 'the optimal temperature for growth', after which growth-rate decreases gradually with a further temperature increase (Brett, 1956; Elliott, 1994). Ambient temperatures of fish living in temperate waters are often encountering water colder than their optimal temperature for growth (Forseth *et al.*, 2009). For instance, in the North Atlantic, *S. salar* typically exploit habitats that are colder than their optimal temperature (Gudjonsson *et al.*, 2015; Minke-Martin *et al.*, 2015), which for post-smolts is about 14 °C (Handeland *et al.*, 2008). Thus, growth usually increases with increasing ambient temperature given that the fish find enough high quality food. However, if resource availability is poor or temperature unusually high, increased temperature can give lower growth because maintenance costs increase with temperature. Furthermore, at temperatures above the optimum, oxygen content in the water becomes a limiting factor for growth (Pörtner, 2010). For instance, *S. salar* exhibit negative growth at temperatures above 25°C because of this (Jonsson *et al.*, 2001).

Fast-growing individuals typically mature younger than conspecifics that grow more slowly (Alm, 1959), except when growth is exceptionally high. In the latter case, maturity can be delayed (Jonsson *et al.*, 1984, 1999). Early maturation is stimulated if the somatic energy density is high, or impeded if the amount of reserved energy is critically low (Mangel & Satterthwaite, 2008). In addition, the effect of increased temperature varies depending on the energy assimilation of the fish. If the energy assimilation is high, higher temperature increases, not decreases size at maturity. The synergistic effect of high temperature and energy food quality was demonstrated in experiments with *S. salar* (Jonsson *et al.*, 2012, 2013). Furthermore, increased growth rate before the onset of maturation, whether this is owing to enhanced lipid content in food or increased water temperature, will decrease age and therefore potentially reduced size at maturity. Thus, within populations of poikilotherms, year-to-year variation in age at maturity can be associated with both ambient temperature and food availability.

The study population, *S. salar* of the Norwegian River Imsa, typically migrate to sea at a body length between 12 and 30 cm, 1-3 years of age (Jonsson & Jonsson, 2014b). They are called smolts at the time of seaward migration, and post-smolts during the first summer and autumn at sea. Most smolts enter seawater during spring and early summer to pursue oceanic feeding. Juveniles entering seawater at other times of the year survive poorly (Hansen & Jonsson, 1989), and when returning to fresh water for spawning, their homing precision is low (Hansen & Jonsson, 1991). The present fish spend 1–2 (seldom 3) years in the ocean until they attain sexual maturity (Jonsson *et al.,* 1991, 2003). When spawning after 1 winter in the ocean, they are called one-sea-winter (1SW) fish, after two or more winters they are called multi-sea-winter (MSW) fish. They return for spawning during autumn freshets between August and October (Jonsson *et al.,* 2007). The majority ascend the river during a period of 4 to 6 weeks. In a warmer climate, the proportion of MSW *S. salar* is expected to increase because of poorer growth, or decrease if feeding opportunities are sufficiently good (Jonsson *et al.,* 2013).

In the present study, we assess life history data on *S. salar* of the River Imsa, monitored from 1976 onwards. Age at maturity is given as proportion of the cohorts that attained maturity as 1SW fish. The mass-length relationship, post-smolt growth and proportion of the seaward migrating fish that return to the home river for spawning were estimated. Based on this, regressions between life history variables and surface temperature in the Eastern Norwegian Sea were tested. Sea surface temperature during the first period in the ocean is important for growth and survival of *S. salar* (Friedland *et al.,* 2009, 2014). Furthermore, each year from 1981 onwards, groups of *S. salar* reared to smolts in a hatchery, wereb released in the river. As brood stock, adults returning to the River Imsa were used. The groups were released to test if environmental conditions influenced wild and released hatchery fish similarly.

Based on life history theory (*e.g.* Roff, 1992), it may be expected that fish length at maturity, mass-length relationship and survival at sea would increase with near-surface temperature during the first year the fish spent at sea. If so, a higher proportion of the cohorts would attain maturity as 1SW fish. However, a complicating factor is that availability of zooplankton has decreased and competition from planktivorous fish, *e.g.* the Norwegian spring spawning herring *Clupea harengus*, have gradually increased gradually during the study period (Beaugrand & Reid, 2012; Huse *et al.,* 2012; Utne *et al.,* 2012). Thus, growth may have decreased and age at maturity increased instead.

MATERIAL AND METHODS

RIVER AND HATCHERY

The River Imsa, South-Western Norway empties into the Boknafjorden near the city of Stavanger (Fig. 1). The river, which is 1 km long, have a restricted spawning area, is characterized by a temperature ranging from 2 to 3 °C in winter and summer maxima of approximately 20 °C. The water discharge ranges from less than 2-3 m^3s^{-1} in summer to autumn maxima of about 10 m^3s^{-1} or more (Jonsson *et al.*, 1989).

In the river, a Wolf trap (Wolf, 1951; apertures 10 mm, inclination 1:10) situated 150 m above the river outlet, catches all descending *S. salar* longer than ca. 10 cm. All ascending fish were captured in a fixed box trap located besides the Wolf trap on top of a three steps fish ladder (Jonsson & Jonsson, 2011). The traps were emptied twice every day during the study period.

The River Imsa hatchery uses river water at slightly elevated temperature that ranges from 2 to 8 °C in winter to approximately 20 °C in summer. Eggs were incubated in Heath vertical stack incubators with a water flow of 4 L min^{-1} and about 1.5 L of eggs per tray. At the onset of feeding, the alevins were transferred to 1-m^2 pools with water depth of 20 cm and water flow of 5.5 L min^{-1}. The young fish were fed EWOS food pellets every 10 minutes during daylight until they reach 10 cm in length, after which they were fed every 20 minutes during daylight. In early June, the hatchery fish were transferred to 4 m^2 pools with a water depth of 50 cm and a flow of about 40 L min^{-1} where they grew for the remainder of the first year. About 50% or more of the fish smolted 1 year old. The remainder were held at the hatchery in 12 m^2 pools with a water flow of 120 L min^{-1} until they smolted 2 year old.

THE FISH

The wild fish originated from adults spawning naturally in the River Imsa during November – December after having completed the entire life cycle in the wild. The embryos incubated through the winter in gravel nests and emerged during the following April. The young (parr) used the river as a nursery before smolting and seaward migration. On average, the wild fish smolted at 1 (14%), 2 (78%) or ≥3 (8%) years of age and migrated into the ocean where most of their growth occurred (Jonsson *et al.*, 1998; Jonsson & Jonsson, 2003). From 1976 to 2010, 36 201 wild smolts migrated from the river to the sea, and tagging studies indicate that they fed in the North Norwegian Sea north of 62°N (Hansen *et al.*, 1993; Jonsson *et al.*, 1993). Of these, 2.9% returned to the trap as adults.

The hatchery fish were reared to smolts from *S. salar* captured in the trap of the River Imsa. Usually more than 10 parents of each sex were used. In early May, the smolts were released at the time when the majority of the wild smolts migrated to sea (Jonsson & Jonsson, 2014b). The release site was located ca. 100 m above the river outlet, just beneath the fish traps in the River Imsa (Jonsson & Jonsson, 2011). Thus, the hatchery fish completed the remainder of their growth to adulthood naturally. During 1981 to 2010, 182 740 1- and 2-year-old hatchery-reared smolts were released. Of these, 1.5% returned to the trap as adults. All adults had similar genetical background within year, as the parental fish were tagged adults returning to the River Imsa, but they may have differ somewhat across years. However, the river is short and the spawning area very restricted and there are therefore only one spawning population in the river.

The released hatchery fish followed the same migratory route and experienced the same marine resources in the North Atlantic as wild *S. salar* (Jonsson *et al.*, 1993). On average, approximately 80% of the adults attained maturity after one winter and two summers in the ocean (1SW), the rest matured as MSW fish, *i.e.* chiefly two winters at sea (Jonsson *et al.*, 1991). As maturing adults, hatchery and wild *S. salar* returned to the Norwegian coast concurrently, but the hatchery fish tended to enter the River Imsa later in the fall than the wild fish (Jonsson *et al.*, 1990).

TREATMENT OF MATERIAL

Before leaving the river, all wild and hatchery *S. salar* were individually tagged with numbered Carlin tags (Carlin, 1955). Natural tip lengths (L, mm; *i.e.* total length of fish with naturally distended caudal fin, Ricker (1979)) and body mass (W, g) were recorded. The fish were anaesthetized with chlorobutanol before being treated, and after treatment, they rested until any visual effect of the anaesthetization had disappear. Then, the fish were returned to the river.

ESTIMATIONS

Post-smolt growth (G) was back-calculated from measurements of the first marine annulus in scales of returning adults caught in the trap (L_{T1} mm) (Jonsson & Stenseth 1976; Jonsson & Jonsson, 2011). From this estimated length we subtracted the smolt length (L_{T0} mm). In total, 668 and 658 scale samples from wild and hatchery-reared fish, respectively, were used: $G = \ln L_{T1} – \ln L_{T0}$.

Fulton's condition factor (*CF*) of the returning adults was calculated as $CF=100 \cdot W/L^3$, where *W* is mass (g) and *L* is natural tip length (cm). This mass-length relationship was used because the individuals were recaptured within a short period in the autumn, were in the same maturity stage and originated from the same population (Wootton, 1998). Bacon *at al.* (2009) evaluated various mass – length relationships and found that for *S. salar*, this simple index gives virtually the same biological interpretation as relationships that are more complex. Furthermore, *CF* of adult *S. salar* caught in the box trap in the River Imsa correlated significantly with their somatic energy density (E KJ 100 g^{-1} wet mass): $E = 8.87 + 553.0\ CF$, $r^2 = 0.44$, df = 1,24, $P < 0.001$. The energy density was measured by summing the energy in proteins, lipids and carbohydrates in the somatic tissue (Craig *et al.*, 1978). Protein was determined by analysis of Kjeldahl. Total lipid content was determined by hydrolysis of a 5-g sample tissue in hydrochloric acid and extraction with diethylether. The carbohydrate content (*i.e.* the total amount of glucose in the sample) was determined according to Mason (1983). These analyses were carried out in triplicate and mean values used. The caloric coefficients for making energy estimates from proximate composition data were 17 kJ in both protein and carbohydrate and 38 kJ in lipid. For more details, see Jonsson & Jonsson (2003).

The majority of the fish attained maturity after 1 winter in the ocean (Jonsson *et al.*, 2003), and MSW fish were excluded from the analyses because they were too few for their findings to be representative except for the last few years. In the tests, mean values of the cohorts were used. When appropriate, similar relationships of individual fish within the cohorts were also tested.

Proportion of the tagged *S. salar* within cohorts that returned to the River Imsa was used as an index of annual sea survival. This was estimated as number of returning adults divided by number of smolts forming the cohort. The figures were not adjusted for any possible mortality effect of tags or tagging, because it was no intention of estimating the absolute survival rate of untagged fish. However, Hansen (1988) found total recapture rates of adult *S. salar* at 7.7% for unmarked, 4.1% for adipose fin-clipped and 3.1% for Carlin tagged smolts, indicating that the survival rate would be more than two times higher for unmarked than Carlin-tagged smolts.

SEA SURFACE TEMPERATURE

Near-surface temperatures (0-10m depth) were retrieved from a several decade's long realization of a hydro-dynamical model resolving the entire Nordic Seas (Lien *et al.*, 2014). A transect consisting of 17 stations (ranging from 62°4' N, 5°2'E off the Norwegian west-coast continuing offshore to 64°7'N, 0° E), in the feeding area of the River Imsa *S. salar*, was applied to represent temperature means in the Norwegian Sea (Fig. 1). This transect was monitored regularly 3-4 times per year by the Norwegian Institute of Marine Research, and the observed temperatures were used to ensure that the model results were unbiased and realistically resolving inter-annual variability. Mean water temperature was estimated for two periods, summer (April through September) and winter (October through March). From April through September is the main growing period of the post-smolts, whereas October through March is a period when growth is low and the fish typically lose weight. In both seasons, sea surface temperature increased significantly during the study period (Fig. 2). Correlations between life history variables and temperature during three months periods were also tested, but these gave no extra information and therefore omitted from the results.

STATISTSICS

The data were analyzed by use of SPSS version 22. Proportional data were not arcsine square root transformed, contrasting the advised by Sokal & Rohlf (1981), because this transformation may produces effects that are difficult to interpret [see Warton & Hui (2011) for a comprehensive argumentation]. However, there was no difference in the general trends and the coefficient of determination of the models were approximately the same, whether or not this transformation was used. Simple linear regression analysis were generally used because the purpose of the study was not to elaborate formal models to explain variability in *S. salar* life history, but to provide simple associations among vital descriptors and time trends. The linear regressions were tested for deviation from normality by use of the Kolmogorov-Smirnov test. Relationships that were significantly correlated, are given in the results. Differences in slopes of the linear regression lines between hatchery produced and wild *S. salar* were tested by use of analysis of covariance (Snedecor & Cochran, 1973). The data series were differenced by one year when comparing life history variables of hatchery and wild cohorts to stabilize the series, because of their monotonic trends. Furthermore, in no case was use of a second independent predictor variable (temperature or life history character) significant in a multiple regression model ($P > 0.05$). For the relationship between proportion of 1SW fish and year of seaward migration, the 4 parameter Weibull equation (Wahed *et al.*, 2009) used, estimated by Python programming (www.Python.org).

RESULTS

The length (L_T) of 1SW *S. salar* of the River Imsa decreased gradually during the study period. This holds for hatchery produced fish released in the river as smolts as well as wild *S. salar* from the river [Fig. 3(a,b)]. For instance, mean length of wild fish decreased from 63 cm to 54 cm, equivalent to a decrease in mass from approximately 2 kg to 1.2 kg (40%). The slopes of the lines differed significantly (comparison of slope; $F_{1,59} = 61.9$, $P < 0.001$). Performing similar analyses for individual fish showed that the variability was large, but the trends were similar and highly significant (Table I).

The condition factor (*CF*) of both released hatchery and wild *S. salar* decreased by 8% [Fig. 3(c,d), comparison of slopes: $F_{1,59} = 2.08$, $P > 0.05$], whereas the post-smolt growth in length decreased faster for hatchery than wild fish [Fig. 3(e,f); comparison of slopes: $F_{1,44} = 13.02$, $P < 0.001$]. Furthermore, *S. salar* exhibited an increase in proportion of 1SW *S. salar* for cohorts migrating to sea before the mid-1990s and a decrease between 2000 and 2010. Similar trends were observed in both wild and hatchery produced fish [Figure 3(g,h)]. For 1SW fish, there was no significant temporal trend in annual survival at sea, in smolt size or growth during the second summer, *i.e.* the year they returned for spawning ($P > 0.05$). Age at maturity as illustrated by the proportion of 1SW fish, increased from the 1970s to the 1990s and decreased again after 2000 to a minimum of about 30% ([Fig. 3(i)]. From the 1980s onwards, the hatchery fish exhibited a similar maturity pattern [Fig. 3(j)]. Similar significant changes in life history traits were observed when individual fish from each cohort was used (Table I).

There were some significant relationships between life history variables and ocean temperatures (Table II), but the coefficient of determination was low exhibiting that only a small proportion of the total variation was explained by the temperature. L_T of 1SW fish decreased with increasing ocean temperature. The slope of the regression was steeper for hatchery than wild *S. salar* [Table II(a), Summer temperature: $F_{1, 57} = 8.8$, $P = 0.005$]. The similar regression between L_T and winter temperature differed in that wild fish exhibited the steepest slope (Winter temperature: $F_{1,57} = 9.1$, $P = 0.004$). Furthermore, body mass relative to length (*CF*) tended to be higher in years when near-surface water in the Norwegian Sea was relatively cold. The slopes of the corresponding regressions did not differ significantly between hatchery and wild fish [Table II (a): Summer temperature, $F_{1,58} = 3.10$, $P > 0.05$, Winter temperature $F_{1,59} = 3.64$, $P > 0.05$]. In addition, a higher proportion of the cohorts of hatchery *S. salar* attained maturity as 1SW fish when the ocean was relatively cold. This holds for both winter and summer temperature when tested separately. The corresponding relationships for wild *S. salar*, however, were not significant ($P > 0.05$). There was no significant correlation between sea survival and temperature in the Norwegian Sea.

In both released hatchery and wild *S. salar*, mean L_T increased with growth during the first summer at sea with a steeper slope in wild than hatchery fish ([Table II(b), $F_{1,44} = 7.48$, $P = 0.01$]. Furthermore, the proportion that attained maturity as 1SW fish increased with *CF*. The slope of the regression was steeper in hatchery than in wild fish ($F_{1,55} = 7.2$, $P = 0.01$). In released hatchery, but not in wild fish, the proportion of 1SW fish also increased with growth during the first summer at sea. On the other hand, there was also a positive relationship between the sea survival of the cohort and growth during the first year at sea in wild *S. salar*, but the corresponding relationship was not significant in hatchery *S. salar*.

Among years, there was significant positive correlation between the lengths of wild 1SW fish on corresponding cohorts of released hatchery *S. salar* [Fig. 4(a)]. However, differencing the two time series by one year, gave no significant relationship ($P > 0.05$). Furthermore, *CF* of wild on hatchery *S. salar* were highly correlated (Fig. 4(b)], but lower for hatchery than wild *S. salar*, particularly in years when the condition factor was low. Differencing the two time series reduced the coefficient of determination ($R^2 = 0.35$, $P = 0.001$). Also, the proportion of wild on hatchery *S. salar* returning to the River Imsa as 1SW fish were highly significant [Fig. 4(c)]. The proportion of 1SW *S. salar* was higher in wild *S. salar* in years when relatively few fish attained maturity as 1SW fish, but lower in years when the proportions were high. Differencing the two time series with one year reduced the coefficient of determination ($R^2 = 0.40$, $P = 0.002$). There was no significant correlation between estimated growth rate or survival at sea of hatchery and wild River Imsa *S. salar* ($P > 0.05$).

DISCUSSION

The time-series show that $L_{T,}$ *CF* and post-smolt growth of *S. salar* have decreased since the 1970s. Similar trends are evident in both wild fish and artificially reared fish released as smolts in the river. The consistency of the patterns indicates that the changes are real, and the decrease in size appears associated with reduced post-smolt growth and not with growth as parr in freshwater or during the second summer at sea. Furthermore, this appears not to be an epigenetic effect of thermal conditions during embryonic development (Finstad & Jonsson, 2012; review in Jonsson & Jonsson, 2014a). Jonsson *et al.* (2014) did not find any effect of increased temperature during early ontogeny on either post-smolt growth or age at maturity in experimental tests with *S. salar* of the River Imsa. Selection or genetic drift was probably not important for changes in these ecological characters, as the decrease in body mass has been as large as 40% over only a few generations, and similar trends have been observed elsewhere, as discussed below. Growth and size in fishes are very plastic (*cf.* Wootton, 1998), and phenotypic responses to environmental change are rapid (Jonsson & Jonsson, 2011).

Many species exhibit smaller sizes because of climate change (Sheridan & Bickford, 2011), but the present case may not only be an effect of the rising temperature, as temperature explained little of the variation in these ecological characters. Although significant, the temperature increase has been only approximately 1 °C, which is little, and should not reduce the mass of 1SW salmon by nearly as much as 40%. Instead, reduced feeding can cause such a dramatic decrease, which may be associated with lower primary and secondary production in the pelagic foodweb as argued by Beaugrand & Reid (2012). During the first year at sea, *S. salar* feed largely on pelagic crustaceans (Amphipoda, Euphausiacea) (Jacobsen & Hansen, 2001; Haugland *et al.*, 2006). The abundance of these organisms have decreasing concurrently with an increased abundance of competing pelagic fish (Huse *et al.*, 2012), among which the Norwegian spring spawning *C. harengus* may be the keenest post-smolt competitor. This assumption is indicated by negative correlations between *C. harengus* abundance in the Norwegian Sea and *S. salar* survival (evidence reviewed in Mills, 2003). After the collapse of the Norwegian spring spawning *C. harengus* in 1970, post-smolt growth was particularly good in the 1970s. But as the Norwegian spring spawning *C. harengus* population recovered gradually (Huse *et al.*, 2012; Nøttestad *et al.*, 2015), post-smolt growth has decreased as it has in other European rivers (McCarty *et al.*, 2008; Peyronnet *et al.*, 2008; Friedland *et al.*, 2009).

An additional reason for the decrease in growth and *CF* with time may be the recent increase in abundance of sea lice *Lepeophtheirus salmonis* Burmeister 1834, which may have affected post-smolt growth negatively (Stien *et al.*, 2005). The increased abundance of *L. salmonis* is probably a consequence of the growth of the *S. salar* farming industry since the 1970s (Ford & Myers, 2008). For instance, Gargan *et al.* (2012) reported that *L. salmonis* can induce considerable mortality on *S. salar.* Moreover, Skilbrei *et al.* (2013) found 6 % larger mass of 1SW hatchery-produced *S. salar* treated as smolts either with prophylactic substances emamectin benzoate or EX (Pharmac), against *L. salmonis* prior to release in nature, compared with untreated control groups. A similar effect of *L. salmonis* may have reduced growth of the present *S. salar*. However, the reported effect of the *L. salmonis* treatment was much smaller than the 40% decrease in mass found in the present study, and no parallel increase in mortality was observed. Thus, *L. salmonis* may not be a major contributor to the decrease in fish size in the present population.

Todd *et al.* (2008) reported a similar decrease in *CF* of 1SW *S. salar* from Scotland towards the end of the twentieth and beginning of the twenty-first century. They related reduced *CF* and lipid density of the fish to increased sea surface temperature, associated with a recent climate-driven change in the eastern North Atlantic pelagic ecosystem. Furthermore, they see parallels with this decrease to effects on other top consumers, such as Atlantic bluefin tuna *Thunnus thynnus* (L. 1758) and seabirds (Todd *et al.*, 2008). The decreased *CF* of the present *S. salar* indicates a similar reduction in lipid deposits, as the *CF* correlates significantly with the lipid density of the returning adults in the River Imsa. A similar correlation was found for *S. salar* spawning in the Norwegian River Drammen (Jonsson *et al.*, 1997). Thus, the climate-driven ecosystem change may have had a similar effect on the present Norwegian *S. salar* as reported from Scotland, indicating that this is a general trend in the Northeast Atlantic.

Although reduced energy assimilation of the post-smolts may be the prime reason for the decrease in growth, temperature may still have had a contributing effect because of associated metabolic costs. Friedland & Todd (2012) reported that *S. salar* growth was associated with temperature during winter and spring. Furthermore, Hokkaido chum salmon *Oncorhynchus keta* (Walbaum 1792) have had elevated growth and survival rates since the 1980s (opposite to the present results). They assumed that this was a direct effect of higher surface temperature because of global warming (Kaeriyama *et al.*, 2014). In addition, the growth of Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792) in Alaska appears strongly influenced by oceanic winter temperatures (Wells *et al.*, 2008). Thus, the possibility that increased temperature may have had an additional effect on the ongoing change in size and growth of *S salar*, cannot be rejected.

Age at maturity varied during the study period. First, the proportion of 1SW fish increased, but after 2000, it decreased. Age at maturity is highly influenced by growth and size of the fish (Alm, 1959; Jonsson *et al.*, 1984) and for *S. salar*, Friedland & Haas (1996) indicated that late summer growth of the post-smolts was higher in *S. salar* maturing as 1SW than 2SW fish. Furthermore, Salminen (1997) reported that good feeding opportunities gave relatively more 1SW *S. salar* than do poorer feeding opportunities in the Baltic Sea. For released hatchery *S. salar*, they found a significant relationship between early maturation and post-smolt growth, as also found in rearing experiments with the River Imsa salmon (Jonsson *et al.*, 2012, 2013). But in the present study, the relatinship was nonlinear.

A hypothesis that may explaining this nonlinearity is that the relatively high proportion of MSW fish in the 1970s was related to the eminent *S. salar* growth during this decade (Jonsson & Jonsson, 2004). Salmonids can delay maturation if growth is unusually good. Ultimately, this may be an inherited response because of an "expected" increase in reproductive success by postponing maturation (because of the increase in size), more than compensating for the expected decrease in survival, as explained by Jonsson & Jonsson (1993). For instance, when juvenile brown trout *Salmo trutta* L. 1758 switch from zoo-benthic to fish feeding, growth rate increases and maturation is delayed relative to those that still feed on zoobenthos (Jonsson *et al.*, 1999). Similarly, very fast-growing *S. salar* can delay maturation relative to conspecifics with more average growth rate (Jonsson & Jonsson, 2004). This relationship between maturation and growth seems to hold across populations (Jonsson *et al.,* 1991) and in other salmonid species (Larsson *et al.*, 2005; Forseth *et al.,* 2009). Thus, extremely high post-smolt growth may have contributed to the elevated proportion of MSW fish in the 1970s.

However, maturation can also be delayed if growth rate is poor (Alm, 1959), which may be the situation after 2000. In this period, post-smolt growth was low and a gradually increasing proportion of the cohorts may have lacked the needed energy resources to carry out the return migration and spawn successfully as 1SW fish, relative to the requirements of their genetic programme. Furthermore, maturation can be delayed if lipid densities are low (Rowe & Thorpe, 1991; Duston & Saunders, 1999). This holds also for a number of other species, such as *S. trutta* L. 1758 (Bohlin *et al.*, 1994), *O. tshawytscha* (Silverstein *et al.,* 1998) and North Sea Plaice *Pleuronectes* platessa L. 1758 (Grift *et al.,* 2007). Hence, both extra high and extra low growth in the post-smolt period may be associated with maturation as MSW fish.

Otero *et al.* (2012) reported a similar decrease in proportion of 1SW *S. salar* after 2000 in other Norwegian *S. salar* populations emphasizing the generality of this finding. They suggested that the increased age at maturity may be explained by the large-scale ecological changes in the Northeast Atlantic pelagic food web affecting post-smolt growth, which appears reasonable, as discussed above.

Salmo salar may have moved farther north for feeding during recent years. Jensen *et al.* (2014) reported that considerable numbers of *S. salar* were observed as far north as the Svalbard Islands, between 78° and 79° N. This is north of the earlier known area of the species. The individuals sampled did not belong to the River Imsa population, but other rivers chiefly in Northern Norway. It is known that feeding areas of salmonids have changed because of large-scale climate-driven ecosystem shifts in the ocean (Nielsen *et al.*, 2013), and this may hold for many other species (*cf.* Pörtner & Peck, 2010). For instance, Potts *et al.* (2014) reported that *Argrosstomus coronus* De la Pylaie 1835 on the African coast changed their distribution area because of global warming. Thus, the possibility that the feeding area may have shifted northwards in association with climate warming cannot be ruled out, and if the area has changed, this may have influenced growth opportunities of *S. salar*.

Marine survival of *S. salar* in the River Imsa decreased with time before 2000 (Jonsson & Jonsson, 2004), but there is no such trend in the present material. This may be associated with fisheries regulation and reduced fishing intensity at sea, particularly on MSW

S. salar (*cf.* Jensen *et al.*, 1999). But the effect of a less intensive fishing on MSW fish probably had minor effect on the size of 1SW fish. Multi-sea-winter *S. salar* feed mainly on pelagic fish such as *C. harengus* (Jacobsen & Hansen, 2001; Haugland *et al.,* 2006), and should not compete keenly with post-smolts for food. So far, there is no evidence of density dependent survival among Atlantic salmon in the ocean (Jonsson *et al.*, 1998). Thus if anything, mean size should have increased with a reduced fishing pressure on relatively large fish, opposite to the observed trend. There is no knowledge about possible genetic effects of reduced fishing in *S.salar* in the ocean (*cf.* Marty *et al.*, 2014; Uusi-Heikkilä *et al.*, 2015).

Survival appeared little influenced by water temperature during the post-smolt period. For instance, there was no support for the hypothesis that mortality changed with increasing temperature for either wild or hatchery produced *S. salar*. This seems not to agree with the general view that survival is closely associated with environmental temperature in fishes (Somero, 2004; Griffiths & Harrod, 2007). In the present case, the effect may be small compared to other sources of mortality, such as predation and parasitism (*e.g.* Hansen *et al.,* 2003). In addition, variation in age at maturity may have affected their survival. On the other hand, the retrospective growth analysis from scales exhibited a positive correlation between first year growth and survival in wild *S. salar*. This parallels observations in other populations of *S. salar* (*e.g.* McCarty *et al.,* 2008; Peyronnets *et al.,* 2008; Friedland *et al.,* 2009) and in other anadromous species such as *S. trutta* (Jonsson & Jonsson, 2009) and Chinook salmon (Woodson *et al.,* 2013). Growth may mediate survival by the functional relationship between post-smolts and their predators as discussed in Jonsson & Jonsson (2009). The first period of marine life may be particularly demanding for the fish with high mortality when slower growing individuals may be lost because of predation, disease or starvation (Wells *et al.,* 2012). Particularly in years when feeding opportunities are poor, large recruits may survive better than smaller conspecifics. Saloniemi *et al.* (2004) and Cross *et al.* (2008) reported that that relatively large body size gave survival benefits for juvenile *S. salar* in years when the mortality was high.

There were close correlation between wild and hatchery-produced *S. salar* concerning *CF* and age at maturity. This indicates that environmental conditions at sea influenced these life history variables similarly, and that life history variation in released hatchery *S. salar* at least partly reflects that of wild fish with similar genetic structure. Thus, hatchery produced *S. salar* may be used as an ecological indicator on production conditions for wild *S. salar* at sea. From the Pacific Northwest, it was reported that in spite of temporal and spatial variation, the general trend in marine survival is similar for both wild and hatchery coho salmon *Oncorhynchus kisutch* (Walbaum 1792) (Coronado & Hilborn, 1998) indicating that this has wider application than for this population.

In all, the present study revealed a significant change in life history of *S. salar* of the River Imsa strain since the 1970s. The main drivers appear to be the ecosystem change with the collapse in the Norwegian spring spawning *C. harengus* and the subsequent rebuilding of the pelagic fish abundance, together with a decrease in large zooplankton abundance and increase in sea-surface temperature in the Norwegian Sea. Smaller energy stores may render *S. salar* more susceptible to parasitism and the distribution area may move northwards where growth opportunities are poorer. The pelagic ecosystem is highly dynamic, and as a predator, the life history of *S.salar* is highly dependent on other species. With large fluctuations in primary and secondary production in the food web, bottom-up effects on *S. salar* and other predators are expected.

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References

Alm, G. (1959). Connection between maturity, size and age in fishes. *Report of the Institute of Freshwater Research Drottningholm* **40,** 5-145.

Atkinson, D. (1994). Temperature and organism size – a biological law for ectotherms? *Advances in Ecological Research* **25,** 1-58.

Bacon, P.J., Palmer, S.C.F., MacLean, J.C., Smith, G.W., Whythe, B.D.M., Gurney, W.S.C. & Youngson, A.F. (2009). Empirical analyses of the length, weight, and condition of adult Atlantic salmon on the return to the Scottish coast between 1963 and 2006. *ICES Journal of Marine Science* **66,** 844-859. doi: 10.1093/icesjms/fsp096

Beaugrand, G. & Reid, P. C. (2012). Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES Journal of Marine Science* **69,** 1549–1562. doi:10.1093/icesjms/fss153

Berrigan, D. & Charnov, E. L. (1994). Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos* **70,** 474–478. doi:10.2307/3545787

Bohlin, T., Dellefors, C. & Faremo, U. (1994). Probability of first sexual maturation of male parr in wild sea-run brown trout (*Salmo trutta)* depends on condition factor 1 yr in advance. *Canadian Journal of Fishers and Aquatic Sciences* **51,** 1920–1926. doi:10.1139/f94-193

Brett, J.R. 1956. Some principles in the thermal requirements of fishes. *Quarterly Review of Biology* **31,** 75-87.

Carlin, B. (1955). Tagging of salmon smolts in the river Lagan. *Report of the Institute of Freshwater Research Drottningholm* **36,** 57-74.

Clarke A. (2003). Costs and consequences of evolutionary temperature adaptation. *Trends in Ecology and Evolution* **18,** 573-581. doi:10.1016/j.tree.2003.08.007

Coronado, C. & Hilborn, R. (1998). Spatial and temporal factors affecting survival in coho salmon (*Oncorhynchus kisutch*) in the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 2067-2077. doi:10.1139/f98-090

Craig, J.F., Kenley, M.J. & Talling, J.F. (1978). Comparative estimations of the energy content of fish tissue from bomb calometry, wet oxidation and proximate analysis. *Freshwater Biology* **8,** 585-590. doi:10.1111/j.1365-2427.1978.tb01480.x

Cross, A.D., Beauchamp, D.A., Myers, K.W. & Moss, J.H. (2008). Early marine growth of pink salmon in Prince William Sound and the coastal Gulf of Alaska during years of low and high survival. *Transaction of the American Fisheries Society* **137,** 927−939. doi:10.1577/T07-015.1

Daufresne, M., Lengfellner, K. & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Science of the United States of America* **106,** 12788–12793. doi:10.1073/pnas.0902080106

Duston, J. & Saunders, R.L. (1999). Effect of winter food depreviation on growth and sexual maturity of Atlantic salmon (*Salmo salar*) in sea-water. *Canadian Journal of Fisheries and Aquatic Sciences* **56,** 201-207. doi:10.1139/f98-165

Elliott, J.M. (1994). *Quantitative Ecology and the Brown Trout*. Oxford, UK: Oxford University Press.

Finstad, A.G. & Jonsson, B. (2012). Effect of incubation temperature on growth performance in Atlantic salmon. *Marine Ecology Progress Series* **454,** 75-82. doi:10.3354/meps09643

Ford, J. S. & Myers, R. A. (2008). A global assessment of salmon aquaculture impacts on wild salmonids. *PLoS biology* **6**(2), e33. doi: 10.1371/journal.pbio.0060033

Forseth, T., Larsson, S., Jensen, A.J., Jonsson, B., Näslund, I. & Berglund, I. (2009). Thermal performance of juvenile brown trout, *Salmo trutta* L.: no support for thermal adaptation hypotheses. *Journal of Fish Biology* **74,** 133–149. doi:10.1111/j.1095-8649.2008.02119.x

Friedland, K.D. & Haas, R.E. (1996). Marine post-smolt growth and age at maturity of Atlantic salmon. *Journal of Fish Biology* **48,** 1-15. doi:10.1111/j.1095-8649.1996.tb01414.x

Friedland, K.D. & Todd, C.D. (2012). Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon. *Polar Biology* **35,** 593-609. doi:10.1007/s00300-011-1105-z

Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Maoileidigh, N.O. & McCarthy, J.L. (2009). The recruitment of Atlantic salmon in Europe. *ICES Journal of Marine Science* **66,** 289-304. doi:10.1093/icesjms/fsn210

Friedland, K.D., Ward, B.R., Welch, D.W. & Hayes, S.A. (2014). Postsmolt growth and thermal regime define the marine survival of steelhead from the Keogh River, British

Columbia. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* **6,** 1-11. doi:10.1080/19425120.2013.860065

Gargan, P.G., Forde, G., Hazon, N., Russell, D.J.F. & Todd, C.D. (2012). Evidence for sea lice-induced marine mortality of Atlantic salmon (*Salmo salar*) in western Ireland from experimental releases of ranched smolts treated with emamectin benzoate. *Canadian Journal of Fisheries and Aquatic Sciences* **69,** 343-353. doi:10.1139/f2011-155

Griffiths, D. & Harrod, C. (2007). Natural mortality, growth parameters, and environmental temperature in fishes revised. *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 249-255. doi:10.1139/f07-002

Grift, R.E., Heino, M., Rijnsdorp, A.D., Kraak, S.B.M. & Dieckmann, U. (2007). Three-dimensional maturation reaction norms for North Sea plaice. *Marine Ecology Progress Series* **334,** 213-224. doi:10.3354/meps334213

Gudjonsson, S., Einarsson, S.M., Jonsson, I.R. & Gudbrandsson, J. (2015). Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar* L.) as inferred from recoveries of Data Storage Tags. *Canadian Journal of Fisheries and Aquatic Sciences*, early view, doi:10.1139/cjfas-2014-0562

Handeland, S.O., Imsland, A.K. & Stefansson, S.O. (2008). The effect of temperature and fish size on growth, food intake, food conversion efficiency and stomach evacuation rate of Atlantic salmon post-smolts. *Aquaculture* **283,** 36-42. doi:10.1016/j.aquaculture.2008.06.042

Hansen, L.P. (1988). Effects of Carlin tagging and fin clipping on survival of Atlantic salmon (*Salmo salar*) released as smolts. *Aquaculture* **70,** 391-394. doi:10.1016/0044-8486(88)90122-6

Hansen, L.P. & Jonsson, B. (1989). Salmon ranching experiments in the River Imsa: effect of timing of Atlantic salmon (*Salmo salar*) smolt migration. *Aquaculture* **82,** 367-373. doi:10.1016/0044-8486(89)90422-5

Hansen, L.P. & Jonsson, B. (1991). The effect of timing of Atlantic salmon smolt and post-smolt release on the distribution of adult return. *Aquaculture* **98,** 61-67. doi:10.1016/0044-8486(91)90371-D

Hansen, L.P., Holm, M., Holst, J.C. & Jacobsen, J.A. (2003). The ecology of post-smolts of Atlantic salmon. In *Salmon at the Edge* (Mills, D., ed), 25-39. Oxford, UK: Blackwell Science.

Hansen, L.P. Jonsson, N. & Jonsson, B. (1993). Oceanic migration in homing Atlantic salmon. *Animal Behaviour* **45,** 927-941. doi:10.1006/anbe.1993.1112

Haugland, M., Holst, J.C., Holm, M. & Hansen, L.P. (2006). Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES Journal of Marine Sciences* **63,** 1488-1500. doi:10.1016/j.icesjms.2006.06.004

Huse, G., Holst, J. C., Utne, K. R., Nøttestad, L., Melle, W., Slotte, A., Ottersen, G., Fenchel, G. & Uiblein, F. (2012). Effects of interactions between fish populations on ecosystem dynamics in the Norwegian Sea—results of the INFERNO project. *Marine Biology Research* **8,** 415–419. doi: 10.1080/17451000.2011.653372

Jacobsen, J.A. & Hansen, L.P. (2001). Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L. in the Northeast Atlantic. *ICES Journal of Marine Sciences* **58,** 916-933. doi:10.1006/jmsc.2001.1084

Jensen, A. J., Karlsson, S., Fiske, P., Hansen, L.P., Østborg, G.M. & Hindar, K. (2014). Origin and life history of Atlantic salmon (*Salmo salar*) near their northernmost ocean limit. *Canadian Journal of Fisheries and Aquatic Sciences* **71,** 1740-1746. doi:10.1139/cjfas-2014-0169

Jensen, A. J., Zubchenko, A. V., Heggberget, T. G., Hvidsten, N. A., Johnsen, B. O., Kuzmin, O., Loenko, A. A., Lund, R. A., Martynov, V. G., Næsje, T. F., Sharov, A. F. & Økland, F. (1999). Cessation of the Norwegian drift net fishery: changes observed in Norwegian and Russian populations of Atlantic salmon. *ICES Journal of Marine Science* **56,** 84–95. doi:10.1006/jmsc.1998.0419

Jonsson, B. & N. Jonsson (1993). Partial migration: niche shift versus sexual maturation in fishes. *Reviews in Fish Biology and Fisheries* **3,** 348-365. doi:10.1007/BF00043384

Jonsson, B. & Jonsson, N. (2004). Factors affecting marine production of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **61,** 2369-2383. doi:10.1139/f04-215

Jonsson, B. & Jonsson, N. (2009). Migratory timing, marine survival and growth of anadromous brown trout *Salmo trutta* in the River Imsa, Norway. *Journal of Fish Biology* **74,** 621-638. doi: 10.1111/j.1095-8649.2008.02152.x

Jonsson, B. & Jonsson, N. (2011). *Ecology of Atlantic Salmon and Brown Trout: Habitat as a Template for Life Histories*. Fish and Fisheries Series 33, Springer Science & Business Media: Dordrecht, The Netherlands.

Jonsson, B. & Jonsson, N. (2014a). Early environments affect later performances in fishes. *Journal of Fish Biology* **85,** 155-188. doi: 10.1111/jfb.12432

Jonsson, B. & Stenseth, N.C. (1976). Regression of body length on scale size of brown trout, *Salmo trutta*, L. *Norwegian Journal of Zoology* **24,** 331-340.

Jonsson, B., Finstad, A. & Jonsson, N. (2012). Winter temperature and food quality affect age and size at maturity in ectotherms: an experimental test with Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* **69,** 1817-1826. doi:10.1139/f2012-108

Jonsson, B., Forseth, T., Jensen, A.J. & Næsje, T.F. (2001). Thermal performance in juvenile Atlantic salmon, *Salmo salar* L. *Functional Ecology* **15,** 701-711. doi:10.1046/j.0269-8463.2001.00572.x

Jonsson, B., Hindar, K. & Northcote, T.G. (1984). Optimal age at sexual maturity of sympatric and experimentally allopatric cutthroat trout and Dolly Varden charr. *Oecologia* **61,** 319-325. doi:10.1007/BF00379628

Jonsson, B., Jonsson, N. & Finstad, A.G. (2013). Effects of temperature and food quality on age at maturity of ectotherms: an experimental test of Atlantic salmon. *Journal of Animal Ecology* **82,** 201-210. doi:10.1111/j.1365-2656.2012.02022.x.

Jonsson, B., Jonsson, N. & Finstad, A.G. (2014). Linking embryonic temperature with adult reproductive investment. *Marine Ecology Progress Series* **515,** 217-226. doi:10.3354/meps11006

Jonsson, B., Jonsson, N. & Hansen, L.P. (1990). Does juvenile experience affect migration and spawning of adult Atlantic salmon? *Behavioral Ecology and Sociobiology* **26,** 225-230. doi:10.1007/BF00178315

Jonsson, B., Jonsson, N. & Hansen, L.P. (2007). Factors affecting river entry of adult Atlantic salmon in a small river. *Journal of Fish Biology* **71,** 943-956. doi:10.1111/j.1095-8649.2007.01555.x

Jonsson, B., Jonsson, N. & Ruud-Hansen, J. (1989). Downstream displacement and life history variables of Arctic charr (*Salvelinus alpinus*) in a Norwegian river. *Physiology and Ecology Japan, Special volume* **1,** 93-105.

Jonsson, N. & Jonsson, B. (2003). Energy density and content of Atlantic salmon: variation among developmental stages and types of spawners. *Canadian Journal of Fisheries and Aquatic Sciences* **60,** 506-516. doi:10.1139/f03-042

Jonsson, N. & Jonsson, B. (2014b). Time and size at seaward migration influence the sea survival of Atlantic salmon (*Salmo salar* L.). *Journal of Fish Biology* **84,** 1457-1473. doi:10.1111/jfb.12370

Jonsson, N., Hansen, L.P. & Jonsson, B. (1991). Variation in age, size and repeat spawning of adult Atlantic salmon in relation to river discharge. *Journal of Animal Ecology* **60,** 937-947. doi:10.2307/5423

Jonsson, N., Hansen, L.P. & Jonsson, B. (1993). Migratory behaviour and growth of hatchery-reared post-smolt Atlantic salmon *Salmo salar* L. *Journal of Fish Biology* **42,** 435-443. doi:10.1111/j.1095-8649.1993.tb00346.x

Jonsson, N., Jonsson, B. & Hansen, L.P. (1997). Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **66,** 425-436. doi:10.2307/5987

Jonsson, N., Jonsson, B. & Hansen, L.P. (1998a). Long-term study of the ecology of wild Atlantic salmon smolts in a small Norwegian river. *Journal of Fish Biology* **52,** 638-650. doi:10.1111/j.1095-8649.1998.tb02023.x

Jonsson, N., Jonsson, B. & Hansen, L.P. (1998b). The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar. Journal of Animal Ecology* **67,** 751-762. doi:10.1046/j.1365-2656.1998.00237.x

Jonsson, N., Jonsson, B. & Hansen, L.P. (2003). Marine survival and growth of sea ranched and wild Atlantic salmon. *Journal of Applied Ecology* **40,** 900-911. doi:10.1046/j.1365-2664.2003.00851.x

Jonsson, N., Næsje, T.F., Jonsson, B., Saksgård, R. & Sandlund, O.T. (1999). The influence of piscivory on life history traits of brown trout. *Journal of Fish Biology* **55,** 1129-1141. doi:10.1111/j.1095-8649.1999.tb02064.x

Kaeriyama, M., Seo, H. & Qin, Y.X. (2014). Effect of global warming on the life history and population dynamics of Japanese chum salmon. *Fisheries Science* **80,** 251-260. doi:10.1007/s12562-013-0693-7

Larsson, S., Forseth, T., Berglund, I., Jensen, A.J., Näslund, I., Elliott, J.M. & Jonsson, B. (2005). Thermal adaptation of Arctic charr: experimental studies of growth in eleven charr populations from Sweden, Norway and Britain. *Freshwater Biology* **50,** 353-368. doi:10.1111/j.1365-2427.2004.01326.x

Lien, V.S., Gusdal, Y. & Vikebø, F.B. (2014). Along-shelf hydrographic anomalies in the Nordic Seas (1960–2011): locally generated or advective signals? *Ocean Dynamics* **64,** 1047-1059. doi:10.1007/s10236-014-0736-3

McCarthy, J.L., Friedland, K.D. & Hansen, L.P. (2008). Monthly indices of the post-smolt growth of Atlantic salmon from the Drammen River, Norway. *Journal of Fish Biology* **72,** 1572-1588. doi:10.1111/j.1095-8649.2008.01820.x

Mangel, M. & Satterthwaite, W.H. (2008). Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation and aquaculture. *Bulletin of Marine Science* **83,** 107-130.

Marty, L., Dieckmann U. & Ernande, B. (2014). Fisheries-induced neutral and adaptive evolution in exploited fish populations and consequences for their adaptive potential. *Evolutionary Applications* **8,** 47-63. doi: 10.1111/eva.12220

Mason, M.J. (1983). Determination of glucose, sucrose, lactose and ethanol in foods and beverages, using immobilized enzyme electrods. *Journal of the Association of Official Analytical Chemists* **66,** 981-984.

Mills, D. (2003) *Salmon at the Edge. Oxford, UK:* Wiley-Blackwell.

Minke-Martin, V., Dempson, J.B., Sheehan, T.F. & Power, M. 2015. Otolith-derived estimates of marine temperature use by West Greenland Atlantic salmon (*Salmo salar). ICES Journal of Marine Science*,,early view, doi: 10.1093/icesjms/fsv033

Nielsen, J.L., Ruggerone, G.T. & Zimmerman, C.E. (2013). Adaptive strategies and life history characteristics in a warming climate: Salmon in the Arctic? *Environmental Biology of Fishes* **96,** 1187-1226. doi:10.1007/s10641-012-0082-6

Nøttestad, L., Krafft, B.A., Anthonypillai, V., Bernasconi, M., Langård, L., Mørk, H.L. & Fernö, A. (2015) Recent changes in distribution and relative abundance of cetaceans in the Norwegian Sea and their relationship with potential prey. *Frontiers in Ecology and Evolution*, early view, doi: 10.3389/fevo.2014.00083

Ohlberger, J., Edeline, E., Vøllestad, L.A., Stenseth, N.C. & Claessen, D. (2011). Temperature-driven regime shifts in the dynamics of sizestructured populations. *The American Naturalist* **177,** 211–223. doi:10.1086/657925

Otero, J., Jensen, A.J., L'Abée-Lund, J.H., Stenseth, N.C., Storvik, G.O. & Vøllestad, L.A. (2012). Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers. *Ecology and Evolution* **2,** 2197-2202. doi:10.1002/ece3.337

Parmesan, C. & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421,** 37-42. doi:10.1038/nature01286

Perrin, N. (1995). About Berrigan and Charnov's life-hitory puzzle. *Oikos* **73,** 137-139. doi:10.2307/3545737

Peyronnet, A., Friedland, K.D. & Maoileidigh, N.O., (2008). Different ocean and climate factors control the marine survival of wild and hatchery Atlantic salmon *Salmo salar* in the north-east Atlantic Ocean. *Journal of Fish Biology* **73,** 945-962. doi:10.1111/j.1095-8649.2008.01984.x

Pörtner, H.O. (2010). Oxygen- and capacity limitation of thermal tolerance: a matrix for integrating climate-related stressor effects in marine systems. *Journal of Experimental Biology* **213,** 881-893. doi:10.1242/jeb.037523

Pörtner, H.O. & Farrell, A.P. (2008). Physiology and climate change. *Science* **322,** 690-692. doi:10.1126/science.1163156

Pörtner, H.O. & Peck, M.A. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology* **77,** 175-1779. doi:10.1111/j.1095-8649.2010.02783.x

Potts, W.M., Henriques, R., Santos, C.V., Munnik, K., Ansorge, I., Dufois, F., Booth, A.J., Kirchner, C., Sauer, W.H.H. & Shaw, P.W. (2014). Ocean warming, a rapid distributional shift, and the hybridization of a coastal fish species. *Global Change Biology* **20,** 2765-2777. doi:10.1111/gcb.12612

Ricker, W.E. (1979). Growth rates and models. In *Fish Physiology*, Vol 8 (Hoar, W.S., Randall, D.J. & Brett, J.R., eds), 677-743. New York, NY: Academic Press.

Roff, D.A. (1992). *Evolution of Life Histories: Theory and Analysis.* New York, NY: Springer Science & Business Media.

Rowe, D.K. & Thorpe, J.E. (1991). Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar)* parr. *Canadian Journal of Fisheries and Aquatic Sciences* **48,** 405–413. doi:10.1139/f91-052

Salminen, M. (1997). Relationships between smolt size, post-smolt growth and sea age at maturity in Atlantic salmon ranched in the Baltic Sea. *Journal of Applied Ichthyology* **13,** 121-130. doi:10.1111/j.1439-0426.1997.tb00111.x

Saloniemi, I., Jokikokko, E., Kallio-Nyberg, I., Jutila, E. & Pasanen, P. (2004). Survival of reared and wild Atlantic salmon smolts: size matters more in bad years. *ICES Journal of Marine Science* **61,** 782−787. doi:10.1016/j.icesjms.2004.03.032

Sheridan, J.A. & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Climate Change* **1,** 401–406. doi:10.1038/nclimate1259

Silverstein, J.T., Shearer, K.D., Dickhoff, W.W. & Plisetskaya, E.M. (1998). Effects of growth and fatness on sexual development of Chinook salmon (*Oncorhynchus tshawytscha*) parr. *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 2376-2382. doi:10.1139/f98-111

Skilbrei, O.T., Finstad, B., Urdal, K., Bakke, G., Kroglund, F. & Strand, R. (2013). Impact of early salmon louse, *Lepeophtheirus salmonis*, infestation and differences in survival and marine growth of sea-ranched Atlantic salmon, *Salmo salar* L., smolts 1997–2009. *Journal of Fish Diseases* **36,** 249-260. doi:10.1111/jfd.12052

Snedecor, G.W. & Cochran, W.G. (1973). *Statistical Methods*, 6th edn. Ames, IA: The Iowa State University Press.

Sokal, R.R. & Rohlf, F.J. (1981). *Biometry*, 2nd edition. New York, NY: W.H. Freeman Publishers.

Somero, G.N. (2004). Adaptation of enzymes to temperature: searching for basic “strategies”. *Comparative Biochemistry and Physiology B* **139,** 321-333. doi:10.1016/j.cbpc.2004.05.003

Stien, A., Bjørn, P.A., Heuch, P.A. & Elston, D.A. (2005) Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. *Marine Ecology Progress Series* **290,** 263-275. doi:10.3354/meps.290263

Todd, C.D., Hughes, S.L., Marshall, C.T., MacLean, J.C., Lonergan, M.E. & Biuw, E.M. (2008). Detrimental effects of recent ocean surface warming on growth condition of

Atlantic salmon. *Global Change Biology* **14,** 958-970. doi:10.1111/j.1365-2486.2007.01522.x

Trip, E.D.L., Clements, K.D., Raubenheimer, D. & Choat, J.H. (2014). Temperature-related variation in growth rate, size, maturation and life span in a marine herbivorous fish over a latitudinal gradient. *Journal of Animal Ecology* **83,** 866-875. doi:10.1111/1365-2656.12183

Uusi-Heikkilä, S., Whiteley, A.R., Kuparinen, A., Matsumura, S., Meinelt, T., Killen, S.S., Bierbach, D., Polverina, G., Ludwig, A. & Arlinghause, R. (2015) The evolutionary legacy of size-selective harvesting extends from genes to populations. *Evolutinary Applications*, early view, doi: 10.1111/eva.12268

Utne, K.R., Huse, G., Ottersen, G., Holst, J.C., Zabavnikov, V., Jacobsen, J.A., Oskarsson, G.J. & Nøttestad, L. (2012). Horizontal distribution and development of planktivorous fish stocks in the Norwegian Sea during summers 1995-2006. *Marine Biology Research* **8,** 420-441. doi:10.1080/17451000.2011.640937

Wahed, A.S., Luong, T.M. & Jeong, J.H. (2009). A new generalization of Weibull distribution with application to a breast cancer data set. *Statistics in Medicine* **28,** 2077–2094. doi: 10.1002/sim.3598

Warton, D.I. & Hui, F.K.C. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology* **92,** 3-10. doi:10.1890/10-0340.1

Wells, B.K., Grimes, C.B., Sneva, J.G., McPherson, S. & Waldvogel, J.B. (2008). Relationships between oceanic conditions and growth of Chinook salmon (*Oncorhynchus tshawytscha*) from California, Washington, and Alaska, USA. *Fisheries Oceanography* **17,** 101-125. doi:10.1111/j.1365-2419.2008.00467.x

Wells, B.K., Santora, J.A., Field, JC., MacFarlane, R.B., Marinovic, B.B. & Sydeman, W.J. (2012). Population dynamics of Chinook salmon *Oncorhynchus tshawytscha* relative to prey availability in the central California coastal region. *Marine Ecology Progress Series* **457,** 125−137. doi:10.3354/meps09727

Wolf, P. A. (1951). A trap for the capture of fish and other organisms moving downstream. *Transactions of the American Fisheries Society* **80,** 41–45. 10.1577/1548-8659(1950)80[41:ATFTCO]2.0.CO;2

Woodson, L.E., Wells, B.K., Weber, P.K., MacFarlane, R.B., Whitman, G.E. & Johnson, R.C. (2013). Size, growth, and origin-dependent mortality of juvenile Chinook salmon *Oncorhynchus tshawytscha* during early ocean residence. *Marine Ecology Progress Series* **487,** 163-175. doi:10.3354/meps10353

Wootton, R.J. (1998). *Ecology of Teleost Fishes*, 2nd edn. Dordrecht, The Netherlands: Kluwer Academic Publishers.

Zuo, W., Moses, M.E., West, G.B., Hou, C. & Brown, J.H. (2012). A general model for effects of temperature on ectotherm ontogenetic growth and development. *Proceedings of the Royal Society London Series B* **279,** 1840–1846. doi:10.1098/rspb.2011.2000

Table 1.Regression of life history variables on year of seaward migration (*Y*) for hatchery produced (H) and wild (W) one-sea-winter *S. salar* of the River Imsa, *L* = Length at maturity, *CF* = Fulton's condition factor, *G* = first year growth. The parameters are given with standard error (±S.E.) and were significant ($P<0.05$). r^2= coefficient of determination, *F*-statistics, d.f. = degrees of freedom, *** = $P<0.001$.

Regression	r^2	*F* – statistics	Degrees of freedom
$L_{\mathrm{H}} = 3680.5\ (\pm\ 3.14.2) - 1.55\ ((\pm 0.16)\ Y$		96.5***	1, 2255
$L_{\mathrm{W}} = 5539.7\ (\pm\ 409.1) - 2.48\ (\pm 0.21)\ Y$		146.1***	1, 830
$CF_{\mathrm{H}} = 2.09\ (\pm 0.50) - 0.001\ Y$		6.93***	1, 2242
$CF_{\mathrm{W}} = 3.58\ (\pm 0.646) - 0.001\ Y$		18.82***	1, 830
$G_{\mathrm{H}} = 13.06\ (\pm 1.60) - 0.006\ (\pm\ 0.001)\ Y$		57.6***	1,662
$G_{\mathrm{W}} = 5.62\ (\pm 1.34) - 0.002\ (\pm 0.001)\ Y$		11.5***	1, 665

Table 2. Significant relationships between life history variables of released hatchery (H) and wild =(W) *S. salar* of the River Imsa strain migrating to sea between 1976 and 2010 and (a) Sea surface temperature, and (b) between life history variables. PM = Proportion (%) of annual cohort that attained maturity as one-sea-winter fish, CF = Fulton's condition factor , L = Total length at maturity (mm), G = Growth during the first year at sea estimated from scale measurements, T_{Su} = Mean temperature at 0-10 m depth from April through September in the Norwegian Sea during the first year the fish were at sea, T_{Wi} = Mean temperature at 0-10 m depth from October through September in the Norwegian Sea during the first year the fish were at sea, S = Percentage of cohort that returned to the River Imsa after feeding in the ocean. The parameters are given with standard error (±S.E.) and were significant ($P<0.05$). r^2 = coefficient of determination, F = F-statistics, d.f. = degrees of freedom, * = P < 0.05, ** = P < 0.01, *** = $P<0.001$.

Regression	r^2	F - statistics	Degrees of freedom
(a) With Sea Surface Temperature			
$L_{\mathrm{H}} = 882.0\ (\pm 111.9) - 29.6\ (\pm 11.6)\ T_{\mathrm{Su}}$	0.20	6.51*	1, 26
$L_{\mathrm{W}} = 857.5\ (\pm 1.27.2) - 28.6\ (\pm 13.28)\ T_{\mathrm{Su}}$	0.13	4.65*	1, 30
$L_{\mathrm{H}} = 902.4\ (\pm 105.8) - 43.7\ (\pm 15.5)\ T_{\mathrm{Wi}}$	0.18	8.21**	1, 27
$L_{\mathrm{W}} = 967.5\ (\pm 102.6) - 55.6\ (\pm 14.8)\ T_{\mathrm{Wi}}$	0.32	14.0***	1, 30
$CF_{\mathrm{H}} = 1.18\ (\pm 0.18) - 0.042\ (\pm 0.019) T_{\mathrm{Su}}$	0.16	5.02*	1, 27

$CF_W = 1.33\ (\pm 0.15) - 0.055\ (\pm 0.016)T_{Su}$	0.29	12.6***	1, 31
$CF_H = 1.27\ (\pm 0.15) - 0.072\ (\pm 0.021)T_{Wi}$	0.29	11.5**	1, 28
$CF_W = 1.18\ (\pm 0.15) - 0.054\ (0.021)T_{Wi}$	0.18	6.59*	1, 31
$PM_H = 272.60\ (\pm 82.11) - 19.72\ (\pm 8.49)\ T_{Su}$	0.18	5.39*	1, 25
$PM_H = 278.31\ (\pm 63.46) - 28.17\ (\pm 9.13)\ T_{Wi}$	0.27	9.52**	1, 26
(b) Between life history variables			
$L_H = 419.64\ (\pm 62.06) + 188.97\ (\pm 65.98)\ G_H$	0.20	5.03*	1, 20
$L_W = 355.14\ (\pm 90.96) + 226.85\ (\pm 87.78)\ G_W$	0.22	6.68*	1, 24
$PM_H = -118.7\ (\pm 51.7) + 260.4\ (\pm 66.66)\ CF_H$	0.37	15.27***	1, 26
$PM_W = -67.3\ (\pm 54.1) + 181.6\ (\pm 68.0)\ CF_W$	0.20	7.14**	1, 29
$PM_H = -71.02\ (\pm 46.00) + 161.54\ (\pm 49.07)\ G_H$	0.35	10.8**	1, 20
$S_W = -6.15\ (\pm 4.31) + 9.61\ (\pm 4.16)\ G_W$	0.18	5.33*	1, 24

Legend to figures

FIG. 1. Northern North Sea and eastern Norwegian Sea with the location of the River Imsa at the Southwest coast of Norway and the transect further north where near-surface temperature values were retrieved.

FIG. 2. Mean surface temperature (0-10 m depth) at 62°N in the Northeast Atlantic Ocean (T °C) during (a) April-September 1976-2010 (Y_S): $T_S = -51.96 (\pm 13.92) + 0.03 (0.007) Y$; $r^2 = 0.39$, $F_{1,31} = 19.5$; $P < 0.001$, (b) October-March 1976-2011(Y_W): $T_W = 50.49 (\pm 9.70) + 0.029 (\pm 0.005) Y$, $r^2 = 0.52$, $F_{1,32} = 35.0$, $P < 0.001$.

FIG. 3. Regressions of wild *S. salar* of the River Imsa cohorts migrating to sea between 1976 and 2010, and hatchery fish produced from the same stock and released when ready for seaward migration between 1981 and 2010, on year of release (Y). (a) Total length at return of 1SW hatchery fish (L_H mm): $L_H = 5582 (\pm 1244) – 2.5 (\pm 0.62) Y$; $r^2 = 0.36$, $F_{1,28} = 16.0$, $P < 0.001$. (b) Total length at return of 1SW wild fish (L_W): $L_W = 6104.1 (\pm 988.0) – 2.77 (\pm 0.50) Y$; $r^2 = 0.51$, $F_{1,30} = 31.2$, $P < 0.001$. (c) Condition factor of hatchery fish (CF_H): $CF_H = 5.95 (\pm 2.04) – 0.003 (\pm 0.001) Y$; $r^2 = 0.19$, $F_{1,28} = 6.46$, $P = 0.02$. (d) Condition factor of wild fish (CF_W): $CF_W = 4.67 (\pm 1.69) – 0.002 (\pm 0.001) Y$; $r^2 = 0.15$, $F_{1,31} = 5.27$, $P = 0.03$. (e) First-year growth estimated from scales of hatchery fish (G_H): $G_H = 12.43 (\pm 2.04) – 0.006 (\pm 0.001) Y$; $r^2 = 0.37$, $F_{1,20} = 11.9$, $P = 0.002$. (f) First-year growth estimated from scales of wild fish (G_W): $G_W = 7.37 (\pm 2.61) – 0.003 (\pm 0.001) Y$; $r^2 = 0.20$, $F_{1,24} = 5.9$, $P = 0.02$. (g) Percent 1SW hatchery fish of adults returning to the River Imsa (PM_H %): $PM_H = 1.16 (\pm 2.04)$(Y –

1909.4)^1.01(±1.13) *exp (–((Y-1909.4)*0.01)^18.43(±1.13)), $R_{4,24}^2 = 0.71$, $P<0.01$. (h) Percent 1SW wild fish of adults returning to the River Imsa (PM_W %): PM_W = 1.93 (±4.45 (*(Y-1950.6)^1.09 (±0.57)*exp (-((Y-1950.6)*0.018 (±0.001))^5.84 (±3.04)), $R_{4,27}^2 = 0.59$, $P < 0.01$.

FIG 4. Regression of (a) total body length of wild (L_W mm) on hatchery produced (L_H mm) River Imsa *S. salar* migrating to sea from 1981 to 2010 and returning as 1SW fish: L_W = 142.4 (±115.1) + 0.73 (±0.19) L_H; $r^2 = 0.37$, $F_{1,25} = 14.3$, $P < 0.001$. (b) Mean condition factors of wild (CF_W) on hatchery produced (CF_H) River Imsa salmon migrating to sea from 1981 to 2010 and returning as 1SW fish (CF_W): CF_W = 0.14 (±0.08) + .85 (±0.11) CF_W; $R^2 =$ 0.70, $F_{1,27} = 62$, $P < 0.001$. (c) Proportion of wild (P_W) on hatchery produced (P_H mm) River Imsa salmon migrating to sea from 1981 to 2010 and returning as 1SW fish: PM_W= 18.3 (±6.3) + 0.57 (±0.07)78PM_H; r^2 =0.71, $F_{1,,24} = 58.1$, $P < 0.001$.

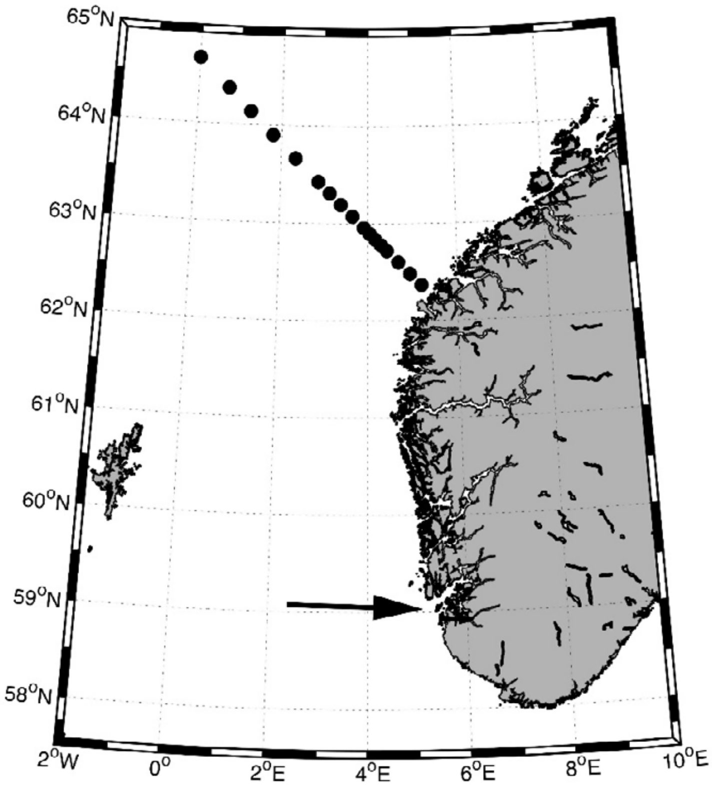


Figure 1.

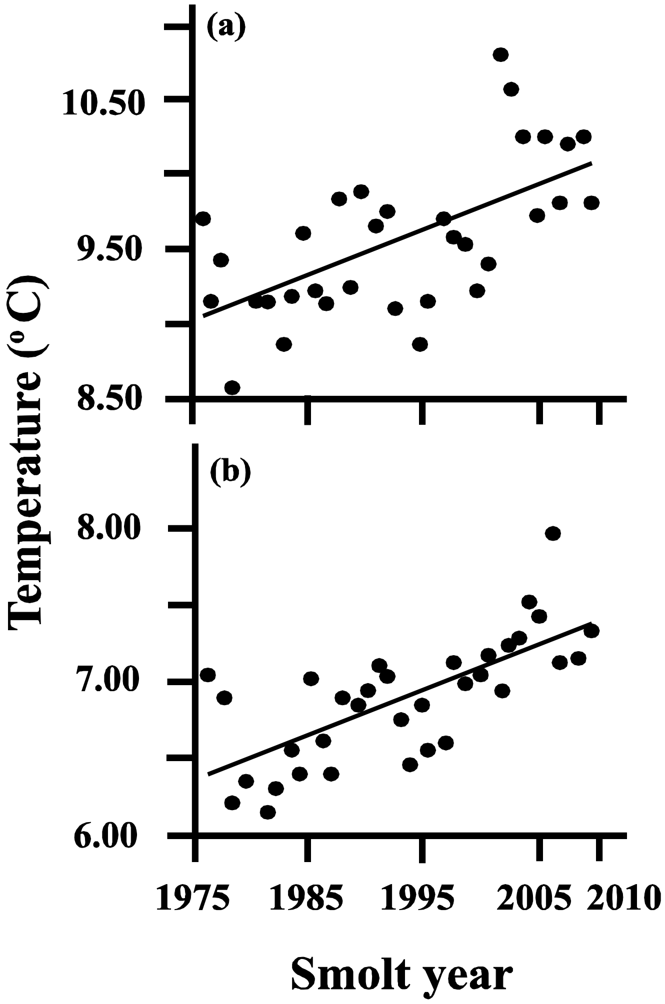
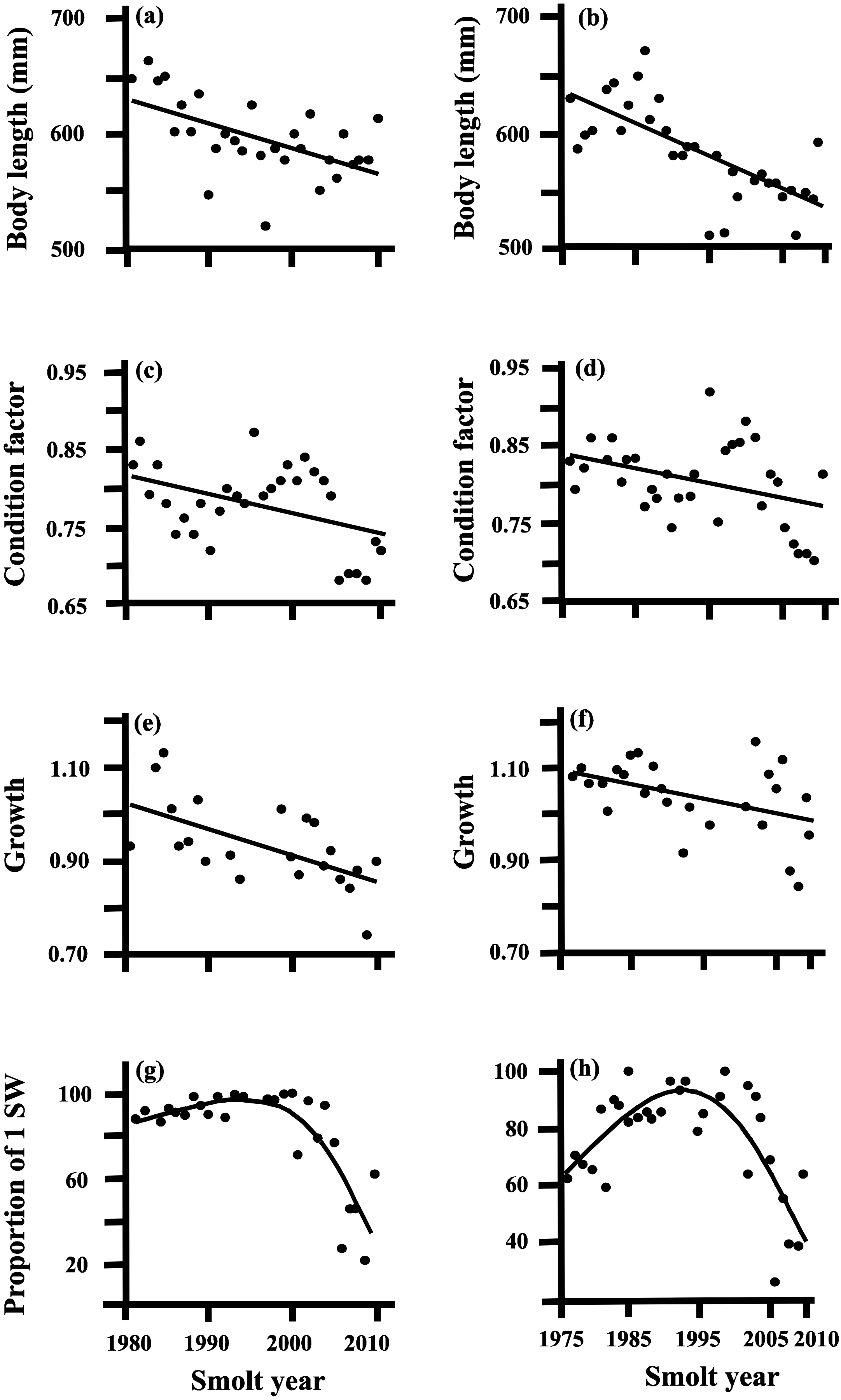

(a)
10.50
9.50
8.50
(b)
8.00
7.00
6.00
Temperature (ºC)
1975
1985
1995
2005
2010
Smolt year

Figure 2.



Body length (mm)
700
600
500
(a)
Body length (mm)
700
600
500
(b)
Condition factor
0.95
0.85
0.75
0.65
(c)
Condition factor
0.95
0.85
0.75
0.65
(d)
Growth
1.10
0.90
0.70
(e)
Growth
1.10
0.90
0.70
(f)
Proportion of 1 SW
100
60
20
(g)
100
80
60
40
(h)
1980
1990
2000
2010
1975
1985
1995
2005
2010
Smolt year
Smolt year

Figure 3.

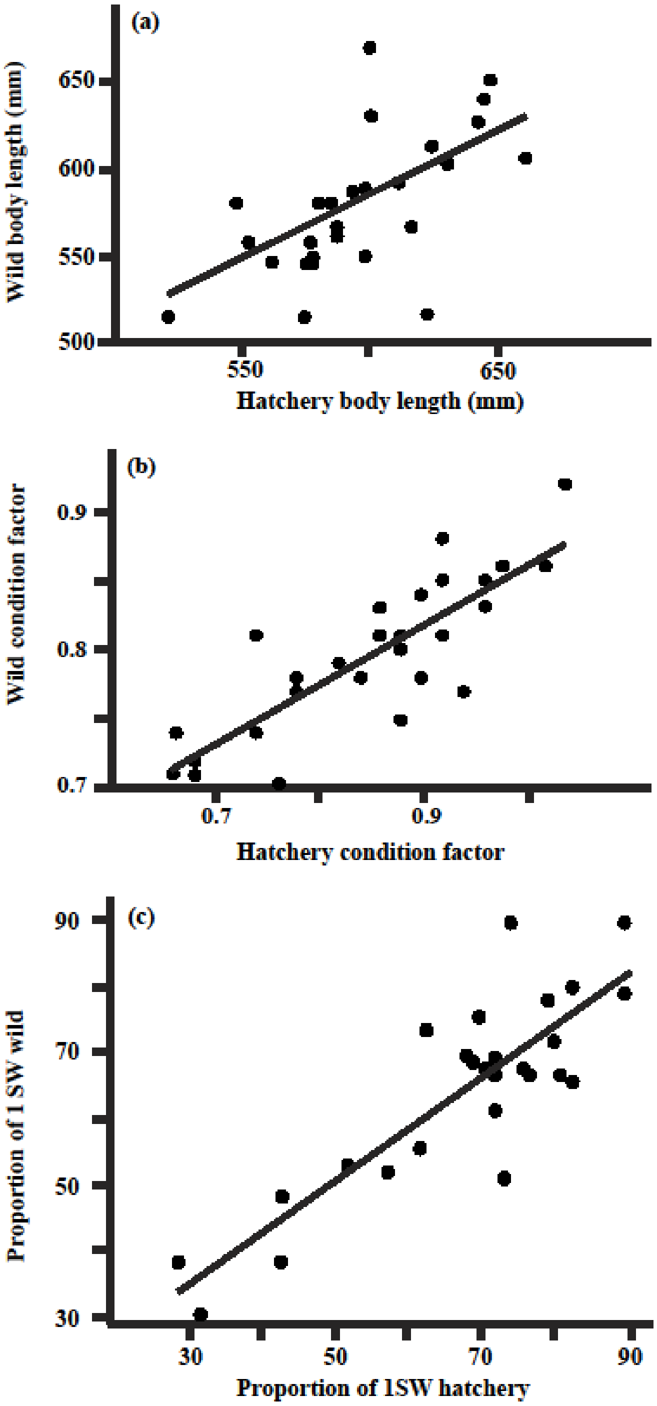

(a)
Wild body length (mm)
650
600
550
500
550
650
Hatchery body length (mm)
(b)
Wild condition factor
0.9
0.8
0.7
0.7
0.9
Hatchery condition factor
(c)
Proportion of 1 SW wild
90
70
50
30
30
50
70
90
Proportion of 1SW hatchery

Figure 4.